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Climate change accelerates range expansion of the invasive non-native species, the Pacific oyster, *Crassostrea gigas*.

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ABSTRACT

Invasive non-native species and global warming are two of the greatest components of global ecosystem change. The Pacific oyster, *Crassostrea gigas*, is the worlds most cultivated shellfish and was introduced throughout the Northwest European Shelf (NWES) under the premise it could not complete its life cycle. Recent warming trends have changed this and wild populations can be found as far north as Nordic Scandinavia. Under the RCP8.5 concentration pathway, we predict the majority NWES coastline will be within *C. gigas*'s thermal recruitment niche by 2100. Given the widespread occurrence of current naturalised *C. gigas* populations, its large larval dispersal potential and a lack of feasible management solutions, *C. gigas* will likely undergo a considerable range expansion this century. The time taken to reach maturity is predicted to decrease by up to 60 days, which may lead to precocious spawning events, facilitating expansion further. *C. gigas* can form extensive reefs completely transforming native systems. This may compromise native biodiversity, protected habitats and commercial species. However, naturalisation can also deliver a number of beneficial ecosystem goods and services to human society. Whether naturalisation is deemed positive or negative will depend on biogeographic context, the perceptions of stakeholders and the wider management priorities.

INTRODUCTION

Anthropogenic warming is causing the redistribution of species at a global scale (Burrows *et al*., 2011; Chen *et al*., 2011; Poloczanska *et al*., 2013). On top of this, humans have directly or indirectly transported species outside their native ranges. The resulting reordering of community structure can have serious ramifications throughout the wider food web that can threaten the intimate link between healthy ecosystem function and human society (Pecl *et al*., 2017). These trends show no sign of abating as temperature rises are predicted to accelerate over the coming decades and invasive non-native species (INNS) eradication attempts are almost impossible after the fact (Norton, 2009; Coumou and Rahmstorf, 2012; Perkins *et al*., 2012). As climate change and INNS introductions represent two of the biggest components of global ecosystem change, predicting when and where ecosystem restructuring will occur is one of the most pressing challenges in conservation and ecosystem management (Walther *et al*., 2009; Butchart *et al*., 2010; Bellard *et al*., 2013).

Correlative species distribution models (SDMs) are the most utilised tool for predicting contemporary and future species distributions. They work by establishing statistical relationships between present day occurrences and underlying environmental variables (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Guisan and Thuiller, 2005). However, they assume contemporary distributions are in equilibrium with the surrounding environment, and as such, it is unknown how much of a species' fundamental niche is represented by its current distribution (Pearson and Dawson, 2003). This means they may perform poorly when extrapolating to invaded and novel regions or future climates (Dormann, 2007; Fitzzpatrck and Hargrove, 2009; Kearney *et al*., 2010). Another limitation is that environmental variables are often entered as static long-term means, rather than instantaneous measures (Bateman *et al*., 2012). This offers little information on dynamic fluctuations of species distributions associated with intra and inter-annual variations. To try and overcome these issues there has been an increasing call for predictions to incorporate underlying physiological mechanisms, based on cause-and-effect relationships (Kearney

and Porter, 2009; Buckley *et al*., 2010, 2011; Evans *et al*., 2015) and high resolution climatic data that incorporates intra and inter-annual variability (Zimmermann *et al*., 2009; Reside *et al*., 2010; Bateman *et al*., 2012). In this way, the ability to predict future species distributions may be significantly increased.

Aquaculture is the world's fasted growing food industry and will be fundamental in future global food production (FAO, 2016). Just like in terrestrial farming, marine species have purposefully been introduced outside of their native ranges due to their ability to grow and survive well in a range of environments. Relocation of bivalves outside of their native ranges has a particularly rich history and some species now have global distributions (McKindsey *et al*., 2007). The Pacific oyster, *Crassostrea* (also known as *Magallana*) *gigas* (Thunberg, 1793), is the world's most globalised bivalve (Ruesink *et al*., 2005; Smaal *et al*., 2018) and has been introduced from its native range in East Asia to over 50 countries. In the NE Atlantic, production is focussed along coastlines of the Northwest European Shelf (NWES), where it was introduced under the premise that it could grow well but conditions were too cold for the successful completion of its life cycle (Troost, 2010). Recent warming trends have changed this, with warmer ocean temperatures during summer now facilitating spawning and settlement in many regions (Thomas *et al*., 2016). This has resulted in naturalisation occurring as far north as southern England and the Skagerrak coasts of Denmark and Norway (e.g. Spencer *et al*., 1994; Dielderich *et al*., 2005; Thomas *et al*., 2016). When naturalised, *C. gigas* can reach high densities and form extensive reefs (e.g. McKnight and Chudleigh, 2015). This can completely transform native habitats and have profound impacts on resident communities (reviewed by Troost, 2010 and Herbert *et al*., 2016). The NWES is also a region of intense socioeconomic importance for fish catches and seafood production and has a network of coastal ecological protections to protect native habitat and species. Therefore, future ecosystem restructuring will have profound implications for commercial enterprise and ecosystem managers.

Here, we take a mechanistic approach to predict the expansion of *C. gigas'* reproductive niche and shifting phenology across the NWES. Specifically, we use known physiological thresholds for spawning and settlement, coupled with high-resolution inter-annual ocean temperature data, to hind cast successful recruitment years (2000 – 2019) and then project how this could change in 20-year time slices up to 2100. We also track the shifting pace in potential spawning date associated with such ocean warming. In doing so, we aim to equip ecosystem managers with the necessary information to make informed choices regarding management strategies of *C. gigas* farms over the coming decades.

METHODS

Predicting *M. gigas'* thermal recruitment niche

Ocean temperature is the most important driver of bivalve fitness and dictates when and where recruitment may occur (Giese, 1959; Philippart *et al*., 2003; Zippay and Helmuth, 2012). While other drivers may interact with temperature to affect recruitment locally (e.g. food availability Gourault *et al*., 2019), temperature is the predominant driver at a regional scale. Indeed, hindcasting approaches have effectively linked ocean warming with recent *C. gigas* recruitment in previously unsuitable areas on the NWES (e.g. Thomas *et al*., 2016). Therefore, using known temperature-recruitment relationships for *C. gigas* is an effective method to gain insight into future climate mediated range expansions at a regional scale.

In order for ectotherm development to progress from one stage to another, certain cumulative heat exposure is required. Past an initiation threshold, ectotherm growth and development increases linearly with temperature. Therefore, the time period needed to achieve a given development stage will vary depending on the temperatures experienced by an individual, and as such, development can be estimated in a cumulative stepwise manner based on daily temperatures the organism experiences. As certain development stages, such as spawning and larval development, have particular heat requirements, development can be estimated based on accumulated degree-days over a given period. Total degree-days are given by:

$$Total\ DD = \int_{day\ 1}^{day\ 365} (T - T_0)\ \ dt \quad \text{for } T > T_0$$

Where *DD* is the number of degree-days, *T* is the ambient temperature in degrees Celcius that the animal is exposed to, T_0 is a threshold temperature below which no development/growth occurs.

For *C.* gigas, Mann, (1979) determined a threshold temperature (T_0) of 10.55°C below which gametogenesis will not occur and a minimum accumulation of DD = 600°C above this level to induce spawning. Whilst lower thermal requirments for spawning have been reported (equivalent to 355 – 397 DD > 10.55 °C) these have been determined from individuals obtained in spring when they may already be partially conditioned (e.g. Helm and Bourne, 2004; Rico-Villa *et al*., 1999). Mann, (1979) used individuals obtained in November, and as such, they had not undergone any previous thermal conditioning before degree-day estimates were derived. Therefore, we use Mann (1979)'s 600 DD requirments > 10.55 °C as our threshold for spawning to occur. However, mature *C. gigas* gonads have also been produced when individuals were conditioned for extensive periods at 8 °C (Fabioux *et al*., 2005). This means our T_0 threshold may be too high, and as such, our estimations of *C. gigas'* TRN are likey conservative. It should also be noted that many *C. gigas* populations are intertidal, and as such, degree-day accumulation for such individuals may also be affected by aerial temperatures not accounted for here.

Recruitment is dependent on larvae developing fully and settling, which has further heat requirements. Based on four previous studies of larval development, Syvret et al. (2008) estimated an additional 225°C degree-days are required for settlement to occur. Here, it is assumed the larval phase shares the same 10.55 °C T_0 threshold required as gametogenesis. How appropriate 10.55 °C is as a baseline for larval development is unknown, as the majority of research has been conducted in hatcheries at high temperatures. However, whilst settlement decreases in laboratrory settings at temperatures < 15 °C (Gillespie *et al*., 2012), larvae have been observed in the field at temperatures as

low as 13 °C (Kulikova *et al*., 2015). As our understading of the viability of larvae at lower temperatrues in the field increases, the larval T_0 may need to be adapted slightly.

Here, we define *C. gigas*'s Thermal Recruitment Niche (TRN) to be 825°C degree-days above 10.55°C (600°C for spawning and 225°C for larval development). To track *C. gigas's* shifting phenology (i.e. the date at which spawning may occur) we use the spawning threshold of 600°C degree-days above 10.55°C. To account for potential uncertainty in reported degree-day estimates, we included a 10% uncertainty envelope in our analysis (Figures S2 and S3).

Climate data

Historic baseline

Ocean bottom temperature data spanning the period 01/01/2000 to 31/12/2018 were derived from the European North West Shelf Ocean Reanalysis system (available from http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=NORTHWESTSHELF_REANALYSIS_PHY_004_009; for a detailed description see http://resources.marine.copernicus.eu/documents/PUM/CMEMS-NWES-PUM-004-009.pdf). The regional ocean model is the FOAM AMM7 (Forecasting Ocean Assimilation Model, 7km resolution Atlantic Margin Model) setup of NEMO (Nucleus for European Modelling of the Ocean) version 3.6, together with the 3DVar NEMOVAR system (version 3) which assimilates observations of sea surface temperatures together with vertical profiles of temperature and salinity. Lateral open boundary forcing was derived from the GloSea5 global ocean reanalysis and at the Baltic margins from the CMEMS Baltic reanalysis. Atmospheric forcing was derived from the ERA-Interim atmospheric reanalysis.

Future temperature

The future projection of ocean temperatures used a dynamical downscaling approach, i.e., a high-resolution (7 km horizontal resolution) regional ocean model (ROM) was forced with

output from a low-resolution Global Climate Model (GCM) (~85 km horizontal resolution) (see next paragraph and Hermans et al., 2020 for details). This approach has several advantages: The GCM fails to capture small-scale topographical and climatological features due to its low resolution and fixed depth levels which, are resolved by the ROM. Furthermore, oceanographic processes important in shallow shelf sea areas, such as tidal mixing or eddie dynamics, are resolved by the ROM.

The ROM used here was the NWES configuration of the ocean model NEMOv3.6, AMM7 setup in configuration CO6 (see O'Dea *et al*., 2017 and Hermans *et al*., 2020 for details) and has a horizontal resolution of 7 km. At the boundaries the ROM was forced with the GCM MOHC-HadGEM2-ES (Collins *et al*., 2011) using the RCP 8.5 concentrations pathway and the model was run from 1972 to 2099. RCP 8.5 was selected to represent a worst-case projection. Ocean bottom temperature was used to calculate the body temperature experienced by oysters, as this is arguably more realistic than using sea surface temperatures. Data were limited to 40 m to represent a maximum depth range for *M. gigas* (FAO, 2007). Ocean bottom temperatures were extracted for the time period 2000–2099, with 2000–2019 being used as the baseline period. The temperature data were bias corrected against the NWES Ocean Reanalysis data (see section Historic Baseline for details) using a reference period of 2000–2018. For the bias correction, a climatology of daily temperatures over a year was calculated at each model grid point as the 7-day running mean of 2000–2018 daily temperatures for both the NWES Ocean Reanalysis data and the future RCP8.5 Northwest European Shelf simulation. The offset between the two climatologies was subtracted at each grid point over the time span of the future simulation for each year.

For our calculations of *M. gigas'* spawning threshold and TRN, we used daily climate data (daily mean temperature) rather than seasonal means, maxima and/or minima. This approach allowed us to capture spatial variability across the NWES together with intra- and inter annual variability in the future projections and enabled cumulative degree-days to be

calculated on a daily basis. This means years where spawning and settlement can occur were determined, as well as the precise date at which thresholds were exceeded. Instead of only giving snapshot future projections at certain dates (e.g. 2050 or 2100), this approach allows the progression, pace and intensity of potential future invasive characteristics to be quantified.

Individual shellfish sites

To place our future projections of potential range expansion in an applied context and track *C. gigas'* shifting reproductive phenology, nine representative shellfish sites were selected (Figure 1; Table S1) where *C. gigas* is currently farmed or where wild populations are established. These spanned eight countries throughout the NWES and covered a range of climatic characteristics. For each site, we tracked the annual increase in total accumulation degree-days, allowing us to determine the dates that thresholds were exceeded and the expanding period over which degree-days could accumulate.

RESULTS

Projected warming of ocean bottom waters

The regional climate model projection, based on an RCP8.5 concentrations pathway, shows increases in bottom seawater temperatures but with spatial variability across the NWES (Figure 2). Ocean bottom temperatures are projected to increase most in the shallow areas in the southern North Sea along the coastlines of northern France (excluding Brittany), The Netherlands, northwest Germany, the west coast of Jutland (Denmark) and southeast England. For the 2040–2059 timeslice, mean ocean bottom temperatures are projected to increase by up to 1.3°C and by the end of the century (2080-2099) warming reaches up to 3.4°C in these regions. Bottom temperature changes are less pronounced along the coastlines of southwest England, Wales and Ireland, where maximum changes reach 1.1°C in the 2040–2059 timeslice and 2.8°C for the 2080–2099 timeslice. For the coasts of

Scotland and Northern Ireland, these values are are estimated to be lower at 0.7°C and 2.0°C, respectively.

The same patterns are reflected in the temperature changes at the representative shellfish sites (Figure S1). Sites located along continental Europe and southeast England (Wilhelmshaven, Agger Tange, Oostershelde, Whitstable and Cancale) all show temperature increases exceeding 3.1°C by the end of the century. Lower temperature increases are seen for Dungarvan, Bergen and Jura. For Jura, the temperature changes are nearly 1°C lower at the end of the century than for the sites with the strongest warming. By ~2060, all sites have exceeded at least 1°C of warming and 2.5°C by 2100, with respect to the 2000–2019 baseline period.

Expansion of area within M. gigas's thermal recruitment niche

Over the baseline period (2000–2019), the frontier of *C. gigas's* TRN was the Solway Firth in Scotland, the Humber estuary in England, Ireland and Skagerrak coasts of Denmark. Settlement thresholds (DD > 825°C) at the limits of *C. gigas's* TRN were exceeded infrequently (< 3 out of 10 years), whereas coastlines of continental Europe (German Bight, Southern Bight and English Channel) and Southern England were exceeded more often (> 7 out of 10 years) (Figure 3, Figure S2 and S3). Generally, *C. gigas*'s TRN was restricted to coastal areas but offshore areas in the southern North Sea around the Southern and German Bight were also suitable.

Under the RCP8.5 concentrations pathway, our simulation predicts the progressive northwards expansion of *C. gigas*'s TRN to the end of the century. Limited expansion is expected between 2020-2039 but during the 2040-2059 time slice *C. gigas*'s TRN will encompass the majority of the Scottish Western Isles. This period also sees thresholds move from infrequently exceeded (< 3 out of 10 years) to exceeded in the majority of years (> 7 out of 10) around Ireland. *C. gigas*'s TRN encompasses the majority of Norway's North Sea coast between 2060-2079 and the east coast of Scotland between 2080-2099. The

offshore island archipelagos of Shetland and Faroe remain unsuitable at the end of the century.

For our representative sites, those situated in continental Europe (Cancale, France; Oosterschelde, Netherlands and Wilhelmshaven, Germany) and southern England (Whitstable) exceeded settlement thresholds every year over the baseline period (Figure 4). For Agger Tange (Denmark) and Dungarvan (Ireland), settlement thresholds were only exceeded infrequently (< 3 out of 10 years). For Grimstad (Norway), Bergen (Norway) and Jura (UK) settlement thresholds were never exceeded during the baseline period.

The projections for Agger Tange show that the settlement threshold will be exceeded every year (10 out of 10 years) by the middle of the century while this occurs in Dungarvan around 10 years later. The settlement thresholds will first be exceeded in Grimstad (Norway) from 2020, rising rapidly until they are exceeded in all years by 2060-2070. Jura (UK) and Bergen (NOR) shared similar projections with thresholds not exceeded until the 2050's and rapidly rising until thresholds are exceeded every year by 2099.

Shifting phenology

The period of the year during which populations can accrue degree-days increased progressively towards 2100 (Figure 5). By 2099, the increase in days that exceed T_0 (> 10.55 °C) ranged from 54 (Wilmershaven, Ger) to 146 (Dungarvan, ROI). For Cancale (France), Dungarvan (ROI) and Whitstable (UK), populations could accrue degree-days for almost 100% of the year by 2100 (Figure 5; Table S2). Spawning thresholds were exceeded in all years over the baseline period for all sites apart from Bergen, Grimstad and Jura where they were exceeded 2, 9 and 1 times respectively. The mean date spawning could occur varied considerably between sites (Table S3). Generally, spawning thresholds were exceeded later at northerly sites and was reflective of the cooler conditions resulting in a slower pace of degree-day accumulation. That said, Jura saw the latest date that spawning thresholds were exceeded (mid November). The mean date the spawning threshold was

exceeded occurred progressively earlier up to 2099. By the end of the century, spawning thresholds are predicted to occur between 27 (Cancale, F) and 60 (Dungarvan, ROI) days earlier.

DISCUSSION

In this study, we have taken a mechanistic approach to predict the expansion of the area within *C. gigas*' thermal recruitment niche (TRN) at its current naturalisation frontier on the Northwest European Shelf. It is challenging to validate our simulations with historic spawning and recruitment events as large-scale observation progammes are lacking. Moreover, just because an area exceeds *C. gigas*'s TRN does not mean recruitment occurred in that year. Indeed, in SE England, recruitment seems less frequent than our simulations would suggest (Herbert *et al*., 2012). Ultimately, such a fine scale understanding of annual recruitment will require a deeper understanding of how ocean temperature interacts with other drivers to affect recruitment locally. Nonetheless, in broad terms, our baseline predictions of area within *C. gigas'* TRN align well with present day distribution records. Areas regularly exceeding settlement thresholds correspond to locations where self-recruiting reefs are found, along the coasts of continental Europe and southern England (Herbert *et al*., 2016). Settlement thresholds were exceeded less frequently further north and correspond to low abundance wild populations reported around Ireland (Kochmann *et al*., 2013) and the Solway Firth in Scotland (Smith *et al*., 2015). Whilst our simulations indicate settlement thresholds were not exceeded along the Norwegian extent of our study, wild populations can be found along Norway's Skagerrak and North Sea coasts (Wrange *et al*., 2010; Anglès d'Auriac *et al*., 2016; Laugen *et al*., 2015). For the Skagerrak, it may be that the temperatures in the shallow inlets and bays are higher than our model suggests, allowing settlement thresholds to be exceeded, or oyster larvae immigrated from warm source populations such as Oslofjord (Norway), Sweden and continental Europe (Anglès d'Auriac *et al*., 2016). For Norway's North Sea populations, distances from these warmer donor sites are likely too great and temperatures still too low for reproduction. Here, it has been

suggested that strong selection pressure and genetic isolation on a relic aquaculture population near Bergen has facilitated natural selection lowering *C. gigas*' TRN here (Anglès d'Auriac *et al*., 2016). However, *in situ* monitoring of the reproductive biology of Norway's Skagerrak and North Sea populations is required to determine the source of these populations.

Under a future climate projected by a RCP8.5 concentrations pathway, we predict a progressive poleward advancement of the area encompassing *C. gigas*'s TRN. By 2100, Ireland, Scotland and Norway will see settlement thresholds move from never or rarely exceeded, to exceeded in the majority of years. This will increase propagule pressure, leading to higher abundances, and will ultimately result in poleward advancement of *C. gigas*'s naturalised distribution. Given our predicted expansion of *C. gigas'* TRN, the widespread nature of wild and farmed populations throughout the NWES and *C. gigas*' large dispersal capacity (Shanks, 2009), it is likely the majority of coastline on the NWES will be available for colonisation by 2100. Overall, this represents a habitat expansion of ~500 km^2 (area within *C. gigas* TRN) and a northward range expansion of 6° of latitude. However, it should be noted that the RCP8.5 concentrations pathway represents a "worst-case scenario" and if greenhouse gas emissions were to drop significantly in the coming decades then ocean temperatures would warm at a slower rate (IPCC, 2013). This means that the subsequent expansion of *C. gigas*' range could also be slower and less intense than shown here. That said, current patterns of energy consumption show little evidence for such a decline and this concentrations pathway is becoming increasingly more likely. Moreover, given the inherent uncertainty in any of the IPCC scenarios the worst-case scenario is a fundamental consideration for policy makers.

Expansion of *C. gigas* can have significant negative impacts on a wide range of habitats (e.g mussel-beds, Kochmann *et al*., 2008; salt marshes, Escapa *et al*., 2004; rocky shores, Krassoi *et al*., 2008; seagrass beds, Wagner *et al*., 2012; polychaete reefs, Dubois *et al*., 2007; mud flats, Trimble *et al*., 2009), and as such, poses a serious concern for managers

346 responsible for the resilience of these ecosystems. As an ecosystem engineer, *C. gigas* can
347 completely transform coastal systems and reduce habitat heterogeneity across different
348 substrates (Herbert *et al*., 2016). This is a particular concern where transformed habitats are
349 protected for their ecological status, or are of commercial interest. For example, many
350 mudflats and rocky reefs are protected under the EU habitats directive
351 (Directive 92/43/EEC), while oysters can completely transform commercial mussel beds
352 (Markert et al., 2010). The options available to managers to prevent *C. gigas* naturalisation
353 are limited to farming sterile oysters or eradication of wild populations (Nell, 2002; McKnight
354 and Chudleigh, 2015), both of which are likely to be undermined by the widespread nature of
355 large source populations and *C. gigas*' extensive dispersal capacity (e.g. Lallias *et al*., 2015;
356 Robins *et al*., 2017; Angles d'Auriac *et al*., 2017). As these interventions are unlikely to
357 prevent expansions, there may need to be a change in attitudes of managing *C. gigas,* away
358 from that of traditional INNS (Hobbs *et al*., 2006; Truitt *et al*., 2015).

359 In some ways, *C. gigas* naturalisation may benefit or safeguard coastal ecosystems of the
360 NWES. Historically, NWES coastlines included dense populations of native European
361 oysters, *Ostrea edulis,* but overfishing and disease decimated populations resulting in a 95%
362 decline in abundance since the 1950s (Thurstan *et al*., 2013; Smyth *et al*., 2020). This
363 decline has resulted in altered benthic assemblages across Europe and has undoubtedly
364 shifted ecosystem function. Where they coexist, *O. edulis* generally occupies the subtidal
365 and *C. gigas* the interidal but they harbour similar epifaunal assemblages (Zwerschke *et al*.,
366 2016) and can provide similar regulating services (Zwerschke *et al*., 2020). Therefore, whilst
367 there is currently a considerable focus on restoration efforts for *O. edulis* across Europe
368 (Pogoda *et al*., 2019), *C. gigas* naturalisation may help restore coastal communities and
369 ecosystem function in a similar manner to the previous state. Moreover, as ocean warming
370 threatens functionally similar native cool-water bivalves (Jones *et al*., 2010; Fly *et al*., 2015)
371 (e.g. *O. edulis* and the blue mussel, *M. edulis*), naturalisation may also safeguard the
372 delivery of provisioning and regulating ecosystem goods and services in the future (Troost,

2010; Christianen *et al*., 2018). In some countries (e.g. The Netherlands), acceptance of *C. gigas* as a "naturalised" species occurred decades ago (Drinkwaard, 1999), and there is increasing discussion on managing *C. gigas* expansion as a natural resource in countries where expansions have occurred more recently (e.g. UK – Herbert *et al*., 2012; Scandinavia – Laugen *et al*., 2015, Mortensen *et al*., 2019). Ultimately, whether the impact of *C. gigas* expansion is deemed positive or negative will depend on biogeographical context (e.g. proximity to vulnerable sites) and the priorities of ecosystem managers.

On top of an expansion of *C. gigas*' TRN, we also predict warming will impact *C. gigas*' phenology. We show that the time needed to exceed the required cumulative heat exposure for spawning (600°C degree-days) across the NWES may decrease by 27 – 60 days by 2099. This is a similar rate (~5 days per decade) as the 8 day shift in spawning date observed for *C. gigas,* at Bourgneuf Bay, France, between 1988 and 2003 (Thomas *et al*., 2016). Such earlier spawning may widen *C. gigas*'s recruitment window, increase propagule pressure and facilitate its expansion further. However, it should be noted that in addition to cumulative heat exposure for gonad development, spawning is also dependent on exceedance of a threshold water temperature (between 16-23°C depending on site location - Pouveau *et al*., 2006; Castaños *et al*., 2009; Gillespie *et al*., 2012; Norgard *et al*., 2014) and often another enviromental trigger (e.g. tidal temperature shcoks – Mills, 2016, high phytoplankton abundance – Ruiz *et al*., 1992, hydrodynamic flow – Bernard *et al*., 2016). Moreover, once spawned the duration of the larval phase can be affected by quality and quantity of microalgal food (Rico-Villa *et al*., 2006). Therefore, whilst cumulative thermal exposure for spawning and settlement may be reached, reaslised recruitment dates will also be dependant on specific water temperatures, other environmental triggers and larval diet.

C. gigas has a global distribution with climate-mediated naturalisation occurring from aquaculture introductions in North America (Andrews, 1979), South America (Escapa *et al*., 2004), South Africa (Robinson *et al*., 2005) and Australia (Ayres, 1991). Therefore, our approach will be of interest to ecosystem managers at *C. gigas*' naturalisation frontiers

across the globe and given the simplicity of our approach can be easily implemented. However, caution should be taken when trying to predict where exactly *C. gigas* reefs may form. Here, a deeper understanding of how ocean temperature interacts with other drivers is required. At a regional scale, recent approaches, incorporating dynamic energy budget theory, show food availability is also fundemental in *C. gigas'* spawning (Thomas *et al.*, 2016). Therefore, a more accurate understanding of *C. gigas'* range expansion will be gained as high-resolution phytoplankton forecasts become available. On a local scale, availability of suitable substrate, local food-web dynamics and connectivity to source populations will be fundamental in predicting where specific reefs may form. It is also important to consider factors that may slow a realised range expasnion despite an expansion of *C. gigas'* TRN. In particular, high summer temperatures, coupled with post-spawning stress and pathogens can make *C. gigas* vulnerable to "summer mortality syndrome", where severe (> 90 %) and rapid (~weeks) population crashes can occur (e.g. Mortensen *et al.*, 2016). *C. gigas* larvae and small recruits are also vulnerable to a range of predators (birds, crabs, gastropods and sea stars) that that may also control its recruitment (e.g. Faasse and Lighthart, 2009). Other aspects of climate change (e.g. ocean acification) or local stressors (e.g. nutrient loading) may also interact with ocean warming in unforeseen ways. Thus, *C. gigas*'s realised expansion will be more complex than the simplification of its thermal window presented here. Nonetheless, our approach is useful tool to anticipate ecological change at a regional scale and serves as an effective early warning for managers. This should be used to facilitate discussion regarding the best way forward to adapt to this expansion.

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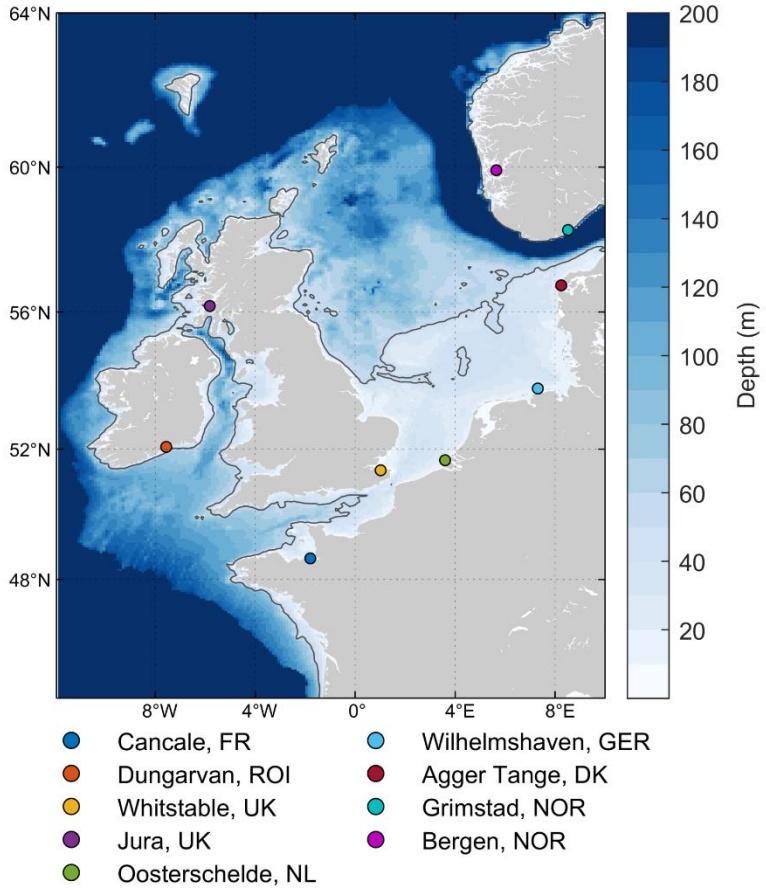


Figure 1. Bathymetry and location of representative *M. gigas* sites within the Northwest European shelf. The black line represents the 40 m depth contour, *M. gigas*' maximum viable depth.

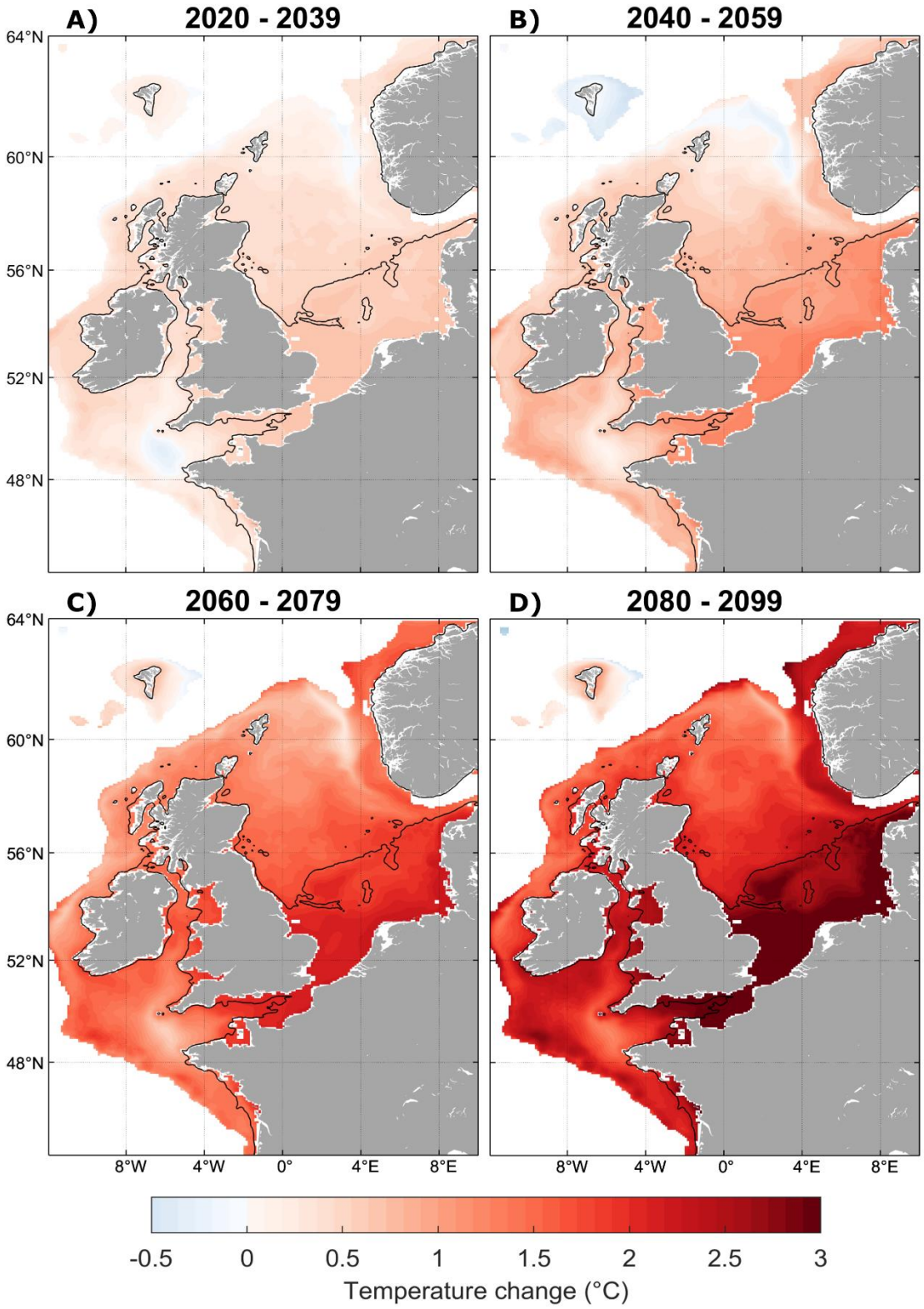


Figure 2. Projected change in ocean bottom water temperatures compared with the baseline period 2000-2019, under an RCP8.5 concentrations pathway, across the Northwest European Shelf in 20 year mean time slices up to 2100. Temperature changes up to a depth of 350 m are shown. The black line denotes the 40 m depth contour which is the maximum viable depth for *C. gigas*.

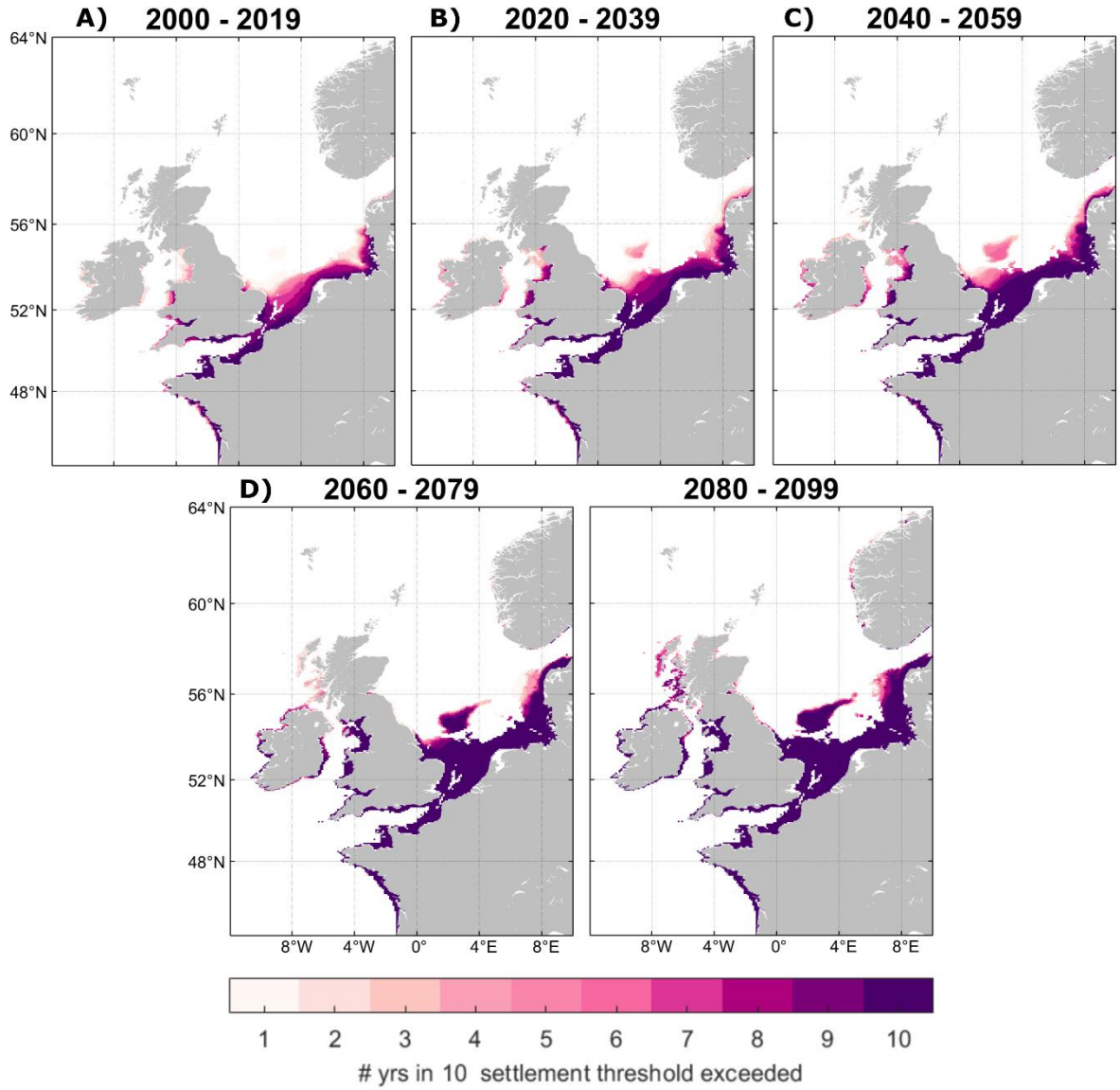
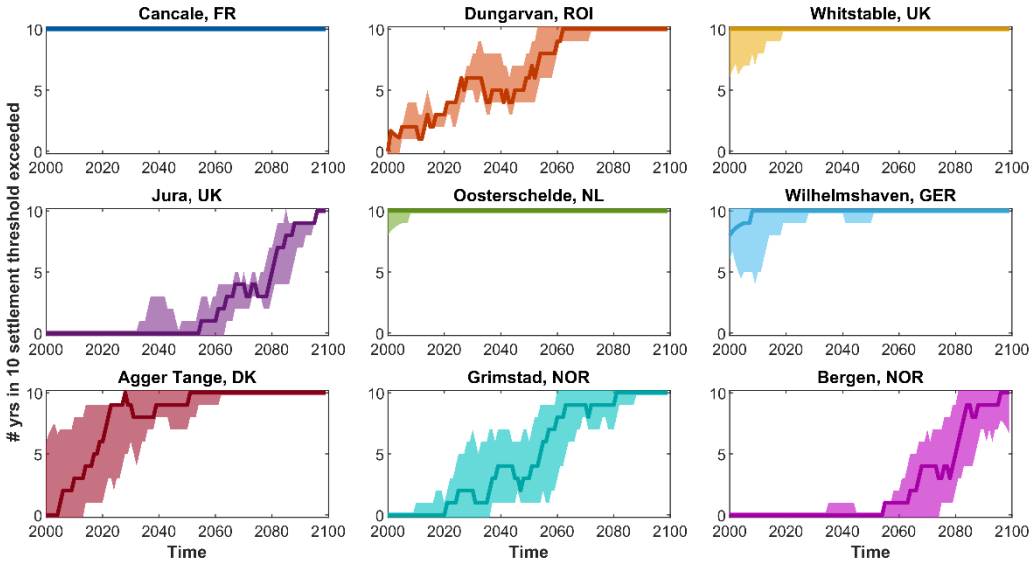


Figure 3. Proportion of years *M. gigas* settlement thresholds (825 degree days above 10.55°C) are exceed for present day baseline period (A: 2000–2019) and future (B-E: 2020–2099) time periods, across the northwest European Shelf. Data limited to 40 m (maximum viable depth of *C. gigas*).



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723 **Figure 4.** Number of years out of 10 years settlement thresholds (825°C degree days above 10.55°C)
724 areexceeded at nine European *C. gigas* population sites from 2000–2100. Shaded area represents +/-
725 10% degree day uncertainty envelope. For site location see Figure 1.
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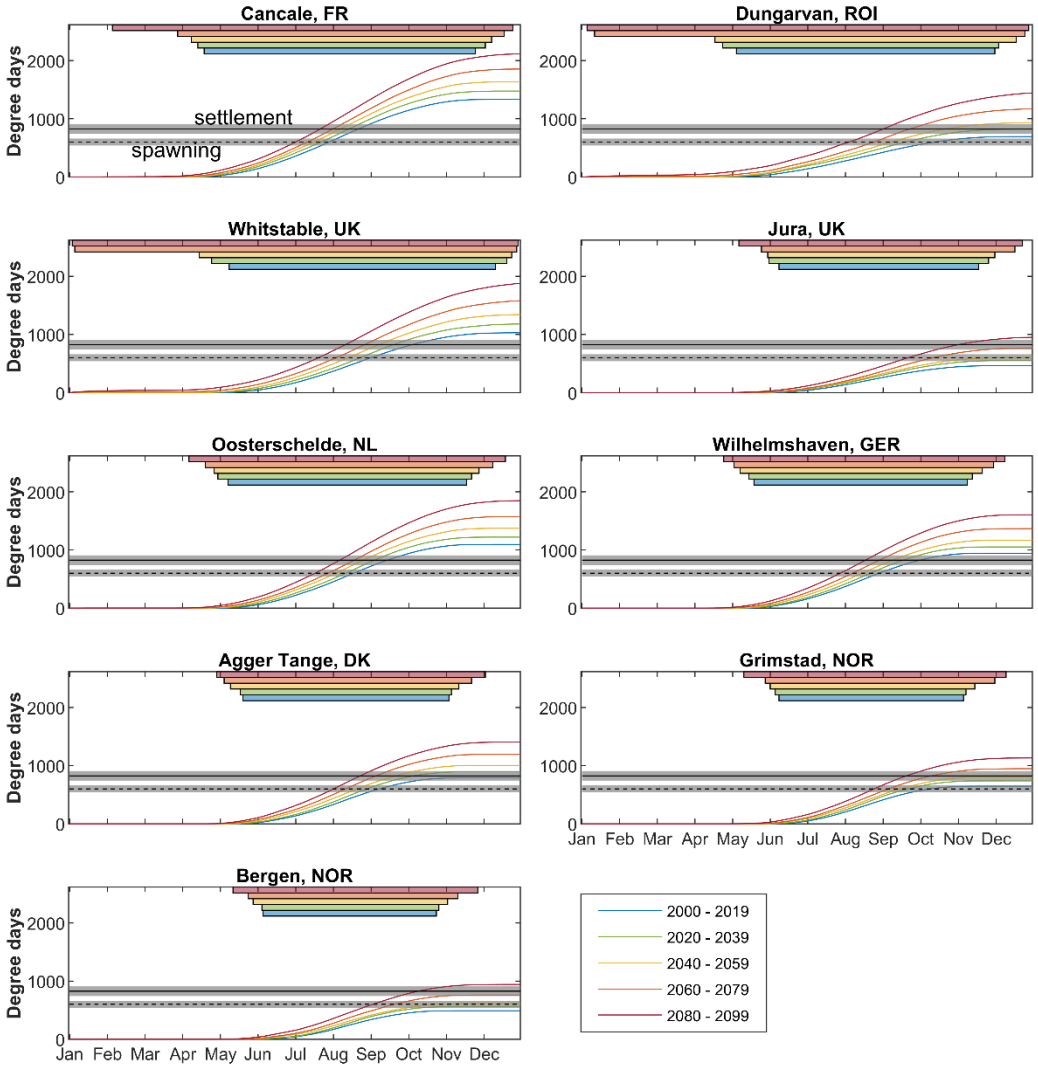

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729 **Figure 5.** Shifting pace toward maturity in *C. gigas* across nine European oyster populations. Line plots show the
730 date at which thresholds are exceeded. Perforated line = spawning threshold (600°C degree days above10.55°C)
731 and solid line = settlement threshold (825°C degree days above 10.55°C). Bar plots show the period over which
732 degree days can be accrued (> 10.55°C). Shaded area represents +/- 10% degree day uncertainty envelope. For
733 site location see Figure 1.
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